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Saine, Sonja

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EFFECTS OF LOCAL FOREST CONTINUITY ON THE DIVERSITY OF FUNGI ON STANDING DEAD PINES

Saine Sonja[1*], Aakala Tuomas[2], Purhonen Jenna[1], Launis Annina[3], Tuovila Hanna[1], Kosonen Timo[4] & Halme Panu[1]

[1] Department of Biological and Environmental Science, University of Jyväskylä, P.O. Box 35, FI-40014 University of Jyväskylä, Finland.
[2] Department of Forest Sciences, University of Helsinki, P.O. Box 27, FI-00014 University of Helsinki, Finland.
[3] Botany unit, Finnish Museum of Natural History, P.O. Box 7, FI-00014 University of Helsinki, Finland.
[4] Herbarium, Biodiversity Unit, University of Turku, FI-20014 Turku, Finland.

*** Corresponding author**
Address: Department of Biological and Environmental Science, University of Jyväskylä, P.O. Box 35, FI-40014, Finland.
Email: sonja.saine@gmail.com

ABSTRACT

Human-induced fragmentation affects forest continuity, i.e. availability of a suitable habitat for the target species over a time period. The dependence of wood-inhabiting fungi on landscape level continuity has been well demonstrated, but the importance of local continuity has remained controversial. In this study, we explored the effects of local forest continuity (microhabitat and stand level) on the diversity of wood-inhabiting fungi on standing dead trunks of Scots pine (*Pinus sylvestris* L.). We studied species richness and community composition of decomposers and *Micarea* lichens on 70 trunks in 14 forests in central Finland that differed in their state of continuity. We used dendrochronological methods to assess the detailed history of each study trunk, i.e. the microhabitat continuity. The stand continuity was estimated as dead wood diversity and past management intensity (number of stumps). We recorded 107 species (91 decomposers, 16 *Micarea* lichens), with a total of 510 occurrences. Using generalized linear mixed models, we found that none of the variables explained decomposer species richness, but that *Micarea* species richness was positively dependent on the time since tree death. Dead wood diversity was the most important variable determining the composition of decomposer communities. For *Micarea* lichens, the community composition was best explained by the combined effect of years from death, site and dead wood diversity. However, these effects were rather tentative. The results are in line with those of previous studies suggesting the restricted significance of local forest continuity for wood-inhabiting fungi. However, standing dead pines that have been available continuously over long periods seem to be important for species-rich communities of *Micarea* lichens. Rare specialists (e.g. on veteran trees) may be more sensitive to local continuity, and should be at the center of future research.

Keywords: dead wood continuity, decomposer, *Micarea*, microhabitat continuity, *Pinus sylvestris* L., stand continuity

1. INTRODUCTION

Intensive forestry activities have led to severe forest fragmentation throughout the globe (Riitters et al., 2000). The spatial aspects of fragmentation, such as decreased habitat amount, size, and connectivity are well known for a negative effect on biodiversity and ecosystems (Bengtsson et al., 2000; Fahrig, 2003). Temporal aspects of fragmentation, such as decreased habitat continuity, have been studied less than the spatial aspects, but have similarly been shown to have negative impacts on biodiversity (Nordén et al., 2014).

Forest continuity can be considered at local level where it relates to longevity of a single, available patch of suitable habitat for the target species or community, and where the scale of habitat patch is equivalent to one local population (Hanski, 2005; Nordén et al., 2014). With higher local continuity, higher species richness and larger variety of specialist species can occur as the colonization and/or breeding probability of species with establishment constraints, slow rates of establishment, development, or growth is enhanced (Esseen et al., 1997; Fritz et al., 2008; Nilsson and Baranowski, 1997; Nordén et al., 2014). The cause for higher species richness and larger variety of specialists may also be the emergence of special microhabitat types confined to late successional phases or larger diversity of different microhabitats. This is due to the absence of large-scale disturbances, which promotes the time-demanding development of these resources (Tibell, 1992; Sverdrup-Thygeson, 2001; Winter and Möller, 2008). Landscape level continuity, on the other hand, refers to a network of available habitat patches within a given region or landscape over time (Fritz et al., 2008; Hanski, 2005; Nordén et al., 2014). Here, the role of dispersal limitations increases when the landscape level continuity decreases (Nordén and Appelqvist, 2001).

Wood-inhabiting fungi are among the organism groups suffering most from the decreased landscape level forest continuity caused by fragmentation (Nordén et al., 2014; Flensted et al., 2016). The importance of this landscape level continuity for wood-inhabiting fungal diversity has been well demonstrated (Flensted et al., 2016; Gu et al., 2002; Junninen and Komonen, 2011; Paltto

et al., 2006; Ranius et al., 2008; Sverdrup-Thygeson and Lindenmayer, 2003). Apparently, the biological reason for this dependence is that some species of wood-inhabiting fungi are in fact dispersal limited (e.g. Norros et al., 2012), although species dependent on ephemeral habitats have a high dispersal ability in general (Herben et al., 1991).

The role of local continuity has remained less clear, compared to landscape level continuity. Stokland and Kauserud (2004) suggested that a polypore *Phellinus nigrolimitatus* cannot effectively colonize suitable trunks when the stand level dead wood continuity decreases. With epiphytic lichens, forest age and continuity appear to have a positive effect on their species richness and affect their community composition (Fritz et al., 2008). Also here, the increased colonization probability with increasing forest age and continuity was considered as the most probable explanation. On the other hand, several studies have detected no effects of local continuity (Groven et al., 2002; Rolstad et al., 2004; Sverdrup-Thygeson and Lindenmayer, 2003), and many studies have been criticized for not demonstrating the effect of continuity *per se* (Nordén and Appelqvist, 2001; Nordén et al., 2014).

In their review, Junninen and Komonen (2011) deduced that boreal polypores are not affected by continuity on a stand scale in any way, and Nordén et al. (2014) concluded that local continuity does not have a significant effect on the diversity of fungi. Nevertheless, this generalization may be misleading; fungi encompass species with divergent ecological characteristics, with many of the species being habitat specialists, requiring dead wood in advanced stages of decay (Nordén et al., 2013). Moreover, studies have not focused on the smallest scale of local continuity, i.e. the detailed history of the microhabitats. Especially the standing dead coniferous trees may retain their qualities for decades, and therefore constitute a microhabitat with potentially high continuity. Considering ephemeral habitats in general, standing dead coniferous trees may be among the slowest constantly changing microhabitats (compared to more persistent abiotically determined microhabitats, such as those in soil).

In this study, we explored the effects of local forest continuity (microhabitat and stand level) on the communities of wood-inhabiting fungi. We studied fungal communities on standing dead wood of Scots pine (*Pinus sylvestris* L., hereafter pine) in 14 forests with varying state of continuity. We used trunk age parameters as estimates for microhabitat continuity, and estimated stand continuity as dead wood diversity and past management intensity. We focused on pine because the species is characterized by slow death and decay process (Niemelä et al., 2002; Siitonen, 2001). Specifically, we asked:

1. How does local forest continuity affect i) species richness and ii) community composition of wood-inhabiting fungi inhabiting standing dead pines?
2. How different scales of continuity (from microhabitat continuity to stand continuity) affect i) species richness and ii) community composition?
3. Are the effects of local continuity different for different fungal groups?

2. MATERIALS AND METHODS

2.1. Study sites and trunk selection

Our 14 study forests (Table 1) were located in central Finland (Fig. 1), 12 of them being in the southern boreal zone, and two in the middle boreal zone (Ahti et al., 1968). In each forest, the study trunks were selected on a 10-m wide transect. Each transect was established 15 meters from the point of easiest access into the study stand. The direction of the transect was towards the center of the stand, except in smaller stands (< 100 m wide) where the transect followed the direction of the longest side of the stand. If the opposite side of a stand was met before trunks were surveyed, the transect was turned around and continued parallel to the first transect. The first five pine trunks within a transect that fulfilled the criteria of being 1) standing (leaning max. 45°) and dead, 2) trunks or high stumps (³ 0.5 m in height), and 3) ³ 7 cm in diameter, were selected for sampling.

Table 1. Site information. Dominant tree species and mean age classes are derived from Natural Resources Institute Finland, 2015.

	Site	Municipality	Dominant tree species	Mean age class
1	Hallinmäki	Jämsä	spruce	96–132
2	Ilmakkamäki	Suonenjoki	pine	56–65
3	Kalaja	Rautalampi	pine	62–71
4	Kirkkokangas	Muurame	spruce	85–109
5	Kivetty	Äänekoski	spruce	72–84
6	Kotinen	Hämeenlinna	spruce	75–89
7	Kuusimäki	Muurame	spruce	45–55
8	Latokuusikko	Kuhmoinen	spruce	88–108
9	Leivonmäki	Joutsa	pine	62–78
10	Lortikka	Kuhmoinen	spruce	70–80
11	Pyhä-Häkki	Saarijärvi	pine	101–144
12	Vaarunvuoret	Jyväskylä	spruce	62–72
13	Vesijako	Padasjoki	spruce	54–63
14	Vuorilampi	Toivakka	pine	45–55

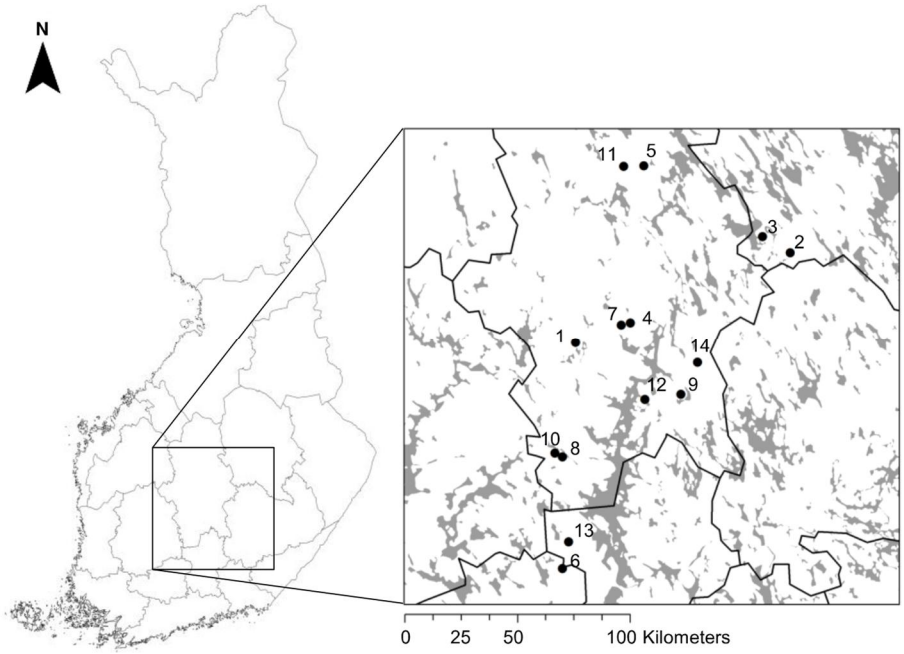


Fig. 1. The map showing the regions of Finland and the locations of the study sites. Site names are presented in Table 1. © National Land Survey of Finland 2016, 2017. [1.5-column fitting image]

2.2. Data collection and preparations

2.2.1. Species data

All decomposer fungi and *Micarea* lichens were recorded from each study trunk based on the occurrence of fruit bodies. Sampling of *Micarea* and *Mycocaliciales* species was conducted in three parts: October 2014, May–June 2015, and September 2015. Rest of the groups (agarics, corticioids,

discomycetes, jelly fungi, polypores, and pyrenomycetes) were sampled in separate surveys in August–September 2015. Agarics were sampled again during October 2015 to meet a better share of a local species community (their detectability is lower than in other groups, see Abrego et al. (2016) and Purhonen et al. (2016)). The trunks were carefully examined throughout from ground level up to a height of 1.8 meters. Species of *Mycocaliciales* were recorded only from sapwood, all other fungal groups also from bark. Fungi were identified to species in the field if possible. Otherwise, specimens were taken for later microscopical identification in the laboratory. Species nomenclature followed Coppins (1983), Czarnota (2007), and Czarnota and Guzow-Krzemínska (2010) with *Micarea* species, Tibell (1999) with species of *Mycocaliciales*, and Index Fungorum (Royal Botanic Gardens Kew et al., 2016) with the rest. If possible, identifications were made to species level, otherwise to genus level.

In the analyses, we used species level identifications. We also included genus level identifications that were different from the identified species of the same genus. We have thoroughly aimed at a similar taxonomic resolution throughout the data. In the case of taxonomically very poorly known groups of *Chaenothecopsis* and *Mycocalium*, several undescribed species were separated based on spore size, type and some other anatomical and chemical characters, and considered as distinct species. Also, some pyrenomycetes remained unidentified, but when it was possible to separate them from the rest of the detected species, they were considered as species in the analyses.

2.2.2. Study trunk specific measures

Several variables were recorded for each study trunk in the field. These included coordinates, circumference at breast height (cm), height (m), decay stage (1–5), the proportion of surface not covered by bark (%) and the coverage of lichens (%). The circumference at breast height was converted to diameter, and it was used as an estimate of survey effort.

We also estimated the canopy openness around the trunks. Four fisheye photos were taken towards principal compass points while standing back against the trunk. The proportion of visible sky was calculated from each photo, using ImageJ (version 1.45s; Schneider et al., 2012). The final estimate for canopy openness was the mean of these four, trunk specific values.

2.2.3. Age and time since death of study trunks

We assigned each study trunk age and time since death, using dendrochronological methods. From each trunk, we extracted a cross-sectional sample disc, or a partial disc. When possible, the samples were extracted from the part of the trunk where bark was still present, to ensure we had the last growth ring. When bark or bark remnants were no longer present, we extracted the sample from where we subjectively estimated minimum ring erosion. In addition to the study trunks, we further extracted increment cores from five live trees within the vicinity of the study trunks at each site, for building a master chronology. In the laboratory, the samples were first dried, increment cores mounted to core mounts, and frail sample discs reinforced following Krusic and Hornbeck (1989; but in normal air pressure). Samples were sanded to make annual rings and ring borders clear and easily observable.

Tree rings were dated, using visual cross-dating (Yamaguchi, 1991), against the site-specific marker rings obtained from the live trees. The widths of the tree-rings in all samples were measured using WinDENDRO (Regent Instruments Inc., 2015), and the visual cross-dating results were statistically confirmed, using the COFECHA-software (Holmes, 1983). If the pith of the tree was missing (necessary for estimating the year of recruitment), we estimated the number of missing rings, using a pith locator (Speer, 2010).

The tree age at death (AAD) was calculated as the difference between the calendar year of the last ring, and the pith year. The years from death (YFD) was calculated as the difference between the sampling year (2015) and the cross-dated year of the last ring. In general, only trunks for which

both variables could be calculated were included in the analyses, but to increase the sample size, we subjectively estimated these variables for six of the trees where the presence of bark could not be ascertained but only a small number of rings were missing. Age at death and years from death for each trunk are presented in Table A.1 in Appendix A.

2.2.4. Dead wood data

2.2.4.1. Dead wood measurements

We collected a dead wood data to estimate the local dead wood continuity in the vicinity of each study trunk. Pieces of dead pine were recorded from four 10 m x 50 m transects, located in principal compass points around each study trunk. Transects to north and south begun at the trunk, and to west and east five meters from the trunk. If more than 10 meters of a transect was unfeasible to locate due to the position of the trunk, two transects were established to the opposite principal compass point. Otherwise the unfeasible part (> 10 m) was turned 90° right. The transect was directed to a feasible half-cardinal point if it was not possible to establish a double transect to the opposite principal compass point.

We included all pieces of dead pine with a diameter of the wider end exceeding 10 cm, and fallen and standing dead wood with length or height ≥ 1 m. A piece of fallen dead wood was recorded only if its base was located inside the transect. The pieces were classified into categories of fallen and standing dead wood (including stumps formed by natural tree fall) and cut stumps. If the identification of tree species was uncertain due to the advanced decay stage, the piece was ignored.

For each piece of dead wood, the maximum diameter was measured. For standing and fallen dead wood, also the height (slant height measured with measuring tape if possible), minimum diameter and decay stage was recorded. A five-point decay stage estimation followed Renvall (1995).

2.2.4.2. Dead wood amount, diversity, and management intensity

Volumes were calculated for each recorded piece of fallen and standing dead wood, using the formula for truncated cone volume. We used the sum of volumes of standing and fallen dead wood in the four transects (total transect area was 1 ha) as the total dead wood volume (m^3 ha^{-1}) on the site. The volumes of study trunks were added up to this estimate, calculated using the formula of right circular cone volume.

The stand continuity was described as diversity index for dead wood, calculated at the site level (Stokland, 2001). For the calculations, we constructed different dead wood types from the combinations of three variables: dead wood category (fallen/standing), canopy position (understory: ø < 30 cm; canopy: ø ≥ 30 cm), and decay stage (1–5). Altogether, there were 20 different dead wood types. The index used was Shannon's diversity index (H) (Shannon and Weaver, 1949):

$$H = -\sum_{i=1}^{s} p_i \, ln \, p_i$$

where p_i is the number of dead wood pieces in a certain dead wood type i (n) divided by the total amount of dead wood pieces (N), and s is the number of different dead wood types.

We used the number of cut stumps per hectare within a site as a measure of forest management intensity, calculated as the sum of stumps recorded from all the transects (sampled area was 1 ha).

2.3. Statistical methods

All analyses were conducted at trunk level separately for decomposers and *Micarea* lichens, and they were performed using R (version 3.3.2; R Core Team, 2016). Dead wood diversity and management intensity were the explanatory variables representing stand continuity, and age at death and years from death represented microhabitat continuity. Dead wood diversity was chosen instead of the dead wood amount as it presumably describes continuity better. Also, diameter and canopy

openness were used to account for variation in survey effort and microclimate (Pouska et al., 2016b), respectively. Every explanatory variable was standardized to mean 0 ± 1 SE. Trunks with missing values in any of the measured variables were omitted from the analyses.

Before the analyses, correlations between explanatory variables were inspected. Tree diameter and age at death correlated strongly (Table A.2 in Appendix A). Age at death was thought to be a more meaningful descriptor of microhabitat continuity of the trunks than diameter, and therefore it was chosen for the analyses of species richness.

A Generalized Linear Mixed Model (GLMM, n = 52) with a Poisson distribution and a log-linear link function was used to study which environmental variables best explained species richness of wood-inhabiting fungi (function “glmer” from the package “lme4” by Bates et al., 2016). Site and trunk identities were included into the models as hierarchically structured random effects by nesting the trunks within sites. The analysis was always started with a full model including all explanatory variables. Then, the model was simplified by removing the least significant variable from the model until only one variable remained. A model with the lowest AIC value was chosen.

We used Bioenv-analysis to study the effects of environmental variables on the community composition (function “bioenv” from the package “vegan” by Oksanen et al., 2017). First, we calculated binary Bray-Curtis dissimilarities for the pairs of communities from the presence-absence transformed species data. All species with only one occurrence and trunks with only one occurring species were excluded from the analyses. In the community data for decomposers, there were 36 species and 48 trunks, and for *Micarea* lichens, 12 species and 33 trunks. We performed Bioenv-analysis to find the best subset of environmental variables (calculated as Euclidean distances) having the highest Spearman rank correlation with the community dissimilarities. To visualize the effects of environmental variables on the community composition, we conducted

Nonmetric Multidimensional Scaling (NMDS) with binary Bray-Curtis dissimilarities (function "metaMDS" from "vegan"). Finally, we chose the best two-dimensional solutions.

We also performed analyses on the responses of 14 individual species, namely those with high enough number of observations for reliable analyses. The methods considering these analyses, as well as their results are presented in Appendix B.

3. RESULTS

3.1. Species richness of wood-inhabiting fungi

Altogether, 107 fungal species were identified with a total of 510 occurrences (Table A.3 in Appendix A). Out of these, 91 were decomposers and 16 *Micarea* lichens (the total number of detected species is somewhat higher than the number included in the analyses because we had to omit the communities for which some environmental variables could not be attained). The mean number of species per trunk was 4.9 for decomposers, and 2.4 for *Micarea* lichens (Table 2). 46 % of the species (n = 49) occurred only once in the data. 21 % (n = 23) of the species had over 5 occurrences, and 15 % (n = 16) had over 10 occurrences. The 5 most common species were *Micarea melaena* (n = 45), *Glonium nitidum* (n = 33), *Micarea prasina* (n = 26), *Micarea misella* (n = 25), and Pyrenomycete sp. 4 (n = 23) (see Table A.3 in Appendix A for a full species list).

Table 2. Site information, showing site level means and standard deviations (in brackets) for stand and trunk level variables (n for AAD and YFD indicated with upper index, for rest of the variables, n = 5 in all sites), and means for all sites. The units used for variables are in brackets. Column label abbreviations: DW = dead wood, stumps = management intensity, AAD = age at death, YFD = years from death, ø = diameter, canopy = canopy openness, dec./trunk = decomposer species richness, lic./trunk = *Micarea* species richness.

		Stand variables			Trunk variables					
	Site	DW div.	Stumps (pc ha^{-1})	DW amount (m^3 ha^{-1})	AAD (y)	YFD (y)	ø (cm)	Canopy (%)	Dec./ trunk	Lic./ trunk
1	Hallinmäki	2.0	94	13.4	130.8^4 (60.9)	25.8^4 (25.7)	17.0 (3.0)	12.2 (2.1)	3.2 (1.8)	1.4 (1.7)
2	Ilmakkamäki	2.3	40	25.2	108.7^3 (12.4)	19.0^3 (9.6)	33.4 (21.2)	15.6 (4.7)	3.0 (3.2)	1.8 (0.8)
3	Kalaja	1.8	30	5.7	147.0^2 (15.6)	12.0^2 (4.2)	31.3 (13.3)	16.8 (4.4)	3.6 (1.8)	3.2 (1.3)
4	Kirkkokangas	1.6	73	68.5	277.1^5 (42.5)	35.6^5 (9.8)	48.7 (9.5)	14.0 (2.7)	6.0 (1.7)	3.6 (1.9)
5	Kivetty	1.6	19	6.9	98.2^5 (10.4)	24.8^5 (7.9)	15.9 (3.7)	16.5 (2.6)	8.4 (1.1)	1.6 (1.5)
6	Kotinen	1.8	26	33.0	236.7^3 (30.6)	41.3^3 (17.9)	29.2 (9.4)	14.3 (3.8)	3.0 (1.2)	2.6 (2.5)
7	Kuusimäki	2.3	16	20.2	147.3^3 (16.6)	33.3^3 (11.7)	27.0 (10.1)	14.7 (1.1)	4.6 (1.1)	2.0 (1.2)
8	Latokuusikko	1.8	36	15.1	166.8^4 (28.6)	45.4^5 (8.2)	28.9 (6.7)	20.3 (5.1)	4.6 (2.4)	2.8 (1.3)
9	Leivonmäki	2.1	106	14.4	111.0^3 (13.5)	32.3^3 (10.3)	30.0 (9.8)	14.9 (3.8)	5.8 (3.1)	1.8 (0.8)
10	Lortikka	1.9	71	3.3	154.8^4 (67.0)	27.0^5 (13.6)	26.8 (5.8)	30.3 (17.2)	4.8 (1.6)	2.0 (2.0)
11	Pyhä-Häkki	2.5	22	61.6	293.3^3 (24.9)	43.3^4 (27.0)	33.4 (12.0)	23.1 (5.5)	6.0 (2.9)	1.6 (1.7)
12	Vaarunvuoret	1.6	112	2.8	144.0^4 (11.0)	31.8^4 (16.7)	24.4 (9.9)	11.8 (1.3)	4.8 (1.9)	2.6 (1.1)
13	Vesijako	2.4	38	25.4	147.0^5 (38.9)	29.8^5 (14.4)	33.7 (7.8)	12.6 (4.7)	5.2 (4.1)	2.8 (2.7)
14	Vuorilampi	2.2	69	22.3	82.8^4 (4.8)	29.0^4 (7.1)	23.8 (12.4)	11.2 (2.9)	5.2 (2.4)	4.0 (1.4)
	All sites	2.0 (0.3)	53.7 (32.3)	22.7 (19.5)	159.9^{52} (70.0)	31.5^{55} (15.3)	28.8 (12.3)	16.3 (7.3)	4.9 (2.5)	2.4 (1.7)

None of the variables entered into the GLMM model affected the decomposer species richness (Table 3), and canopy openness was the only variable remaining in the final model (Table 3; Fig. 2a). For *Micarea* lichens, species richness was positively dependent on years from death (Table 3; Fig. 2b). It was the only variable included in the final model (Table 3).

Table 3. Results from GLMM analysis for species richness of decomposers and *Micarea* lichens (n = 52 for both datasets). Cells show estimates (B), standard errors (SE), z values, and statistical significances (P). Variables having a statistically significant effect are bolded. The units used for variables are in brackets. Abbreviations: canopy = canopy openness, YFD = years from death.

		B	SE	z value	P
Decomposers	**(Intercept)**	1.68	0.08	21.72	< 0.001
	Canopy (%)	0.08	0.08	1.05	0.295
***Micarea* lichens**	**(Intercept)**	0.85	0.11	7.43	< 0.001
	YFD (y)	0.20	0.10	1.98	0.048

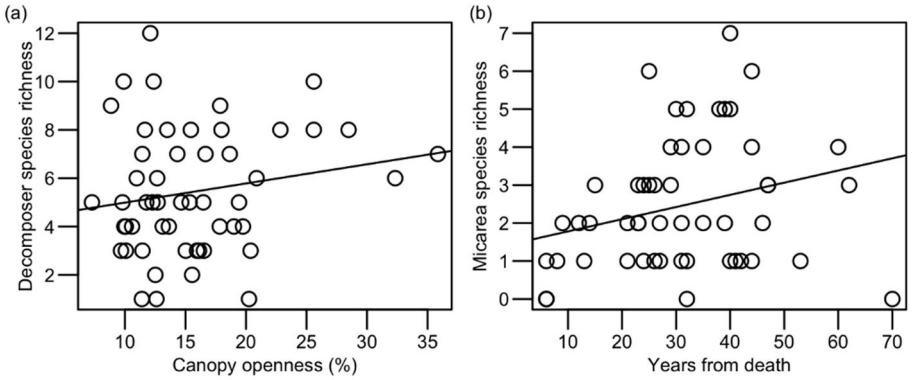


Fig. 2. Responses of (a) decomposer species richness to canopy openness and (b) *Micarea* species richness to the number of years from death. Each dot represents species richness on one trunk. Figures are presented only for variables included in the final models. [1.5-column fitting image]

3.2. Community composition of wood-inhabiting fungi

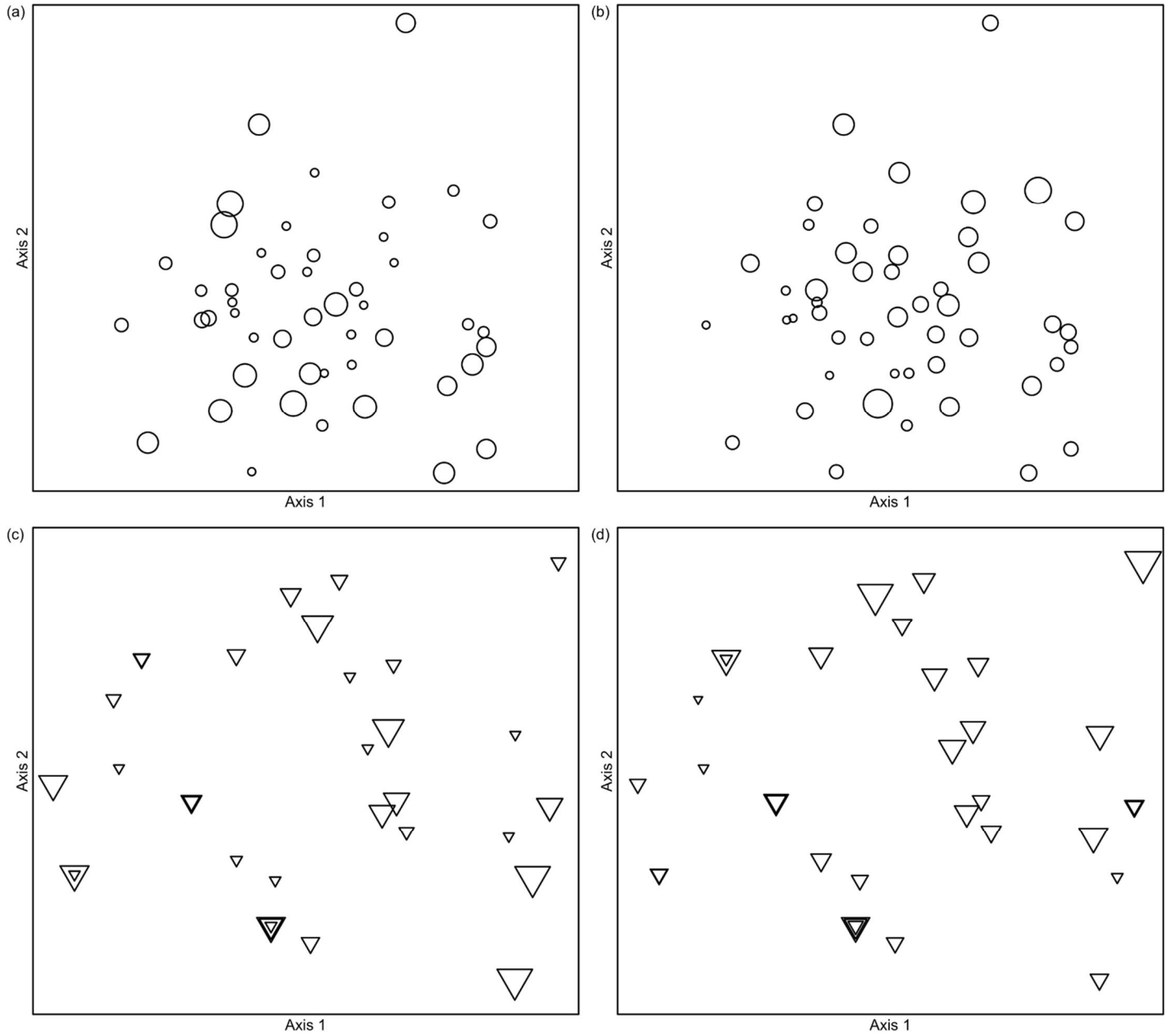
The community composition of decomposers was best explained by dead wood diversity (Table 4; Fig. 3a). In NMDS, communities in the sites with the lowest dead wood diversities were located closer to each other in the center of the ordination space while communities in sites with higher dead wood diversities were more scattered (Fig. 3a). Years from death was the next fitted variable but it did not increase the correlation between the community dissimilarities and environmental distances (Table 4). Nevertheless, in NMDS communities on trunks with the least time since their death had mainly negative values on both axes (Fig. 3b). With increasing time since tree death, communities tended to be located closer to the upper right corner of the ordination space (Fig. 3b). The final stress level for the two-dimensional NMDS solution in Fig. 3a and 3b was 0.175.

The *Micarea* lichen community composition was most efficiently explained by the combined effect of years from death, site and dead wood diversity (Table 4; Fig. 3c and 3d). In NMDS, time

since tree death increased towards the upper right corner of the ordination space (Fig. 3d), and dead wood diversity increased towards the lower right corner of the ordination space (Fig. 3c). However, as adding site increased the correlation between the community dissimilarities and environmental distances, the effect of years from death and dead wood diversity is not independent of site. The final stress level for the two-dimensional NMDS solution in Fig. 3c and 3d was 0.175. Altogether, the results for both decomposers and *Micarea* lichens should be interpreted with caution due to the low correlations in the Bioenv analyses.

Table 4. Results from Bioenv analyses of environmental variables affecting community composition of decomposers and *Micarea* lichens. Correlations are Spearman rank correlations between the community dissimilarities and environmental distances. Abbreviations: DW = dead wood, YFD = years from death, AAD = age at death, Stumps = management intensity, Canopy = canopy openness.

Decomposers		
Size	Variables	Correlation
1	**DW diversity**	**0.128**
2	DW diversity, YFD	0.120
3	DW diversity, YFD, Site	0.109
4	DW diversity, YFD, Site, Diameter	0.099
5	DW diversity, YFD, Site, Diameter, AAD	0.078
6	DW diversity, YFD, Site, Diameter, AAD, Stumps	0.049
7	DW diversity, YFD, Site, Diameter, AAD, Stumps, Canopy	-0.011
***Micarea* lichens**		
Size	Variables	Correlation
1	YFD	0.126
2	YFD, Site	0.168
3	**YFD, Site, DW diversity**	**0.195**
4	YFD, Site, DW diversity, Stumps	0.177
5	YFD, Site, DW diversity, Stumps, AAD	0.160
6	YFD, Site, DW diversity, Stumps, AAD, Canopy	0.142
7	YFD, Site, DW diversity, Stumps, AAD, Canopy, Diameter	0.081



316 **Fig. 3.** NMDS representing the differences in community structure between the communities of decomposers
317 (a–b; circles) and *Micarea* lichens (c–d; triangles) observed in the study. One symbol represents one
318 community occurring on one trunk. The size of a symbol represents the magnitude of dead wood diversity in
319 Fig. 3a and 3c, and the number of years from death in Fig. 3b and 3d. The size of a symbol grows with
320 increasing values of the variables. Stress level for both solutions is 0.175. [2-column fitting image]
321

322 In our analyses on the 14 individual species, four species were statistically significantly
323 affected by some of the variables (Table B.1 in Appendix B). Local continuity explained the
324 presence of the species both positively and negatively. For the rest, the final models did not include

any statistically significant variables. All results considering individual species are presented in Appendix B.

4. DISCUSSION

4.1. Effects of stand continuity

Decomposers and *Micarea* lichens were affected by stand continuity through modest changes in the community composition that were driven by dead wood diversity. Communities of decomposers were more similar among sites with low dead wood diversity and differentiated when dead wood diversity increased. This might be because the communities in sites with low dead wood diversity might have more shared generalist species, able to survive in sites with more homogenous dead wood resources and thus, occurring more evenly across the landscapes (Nordén et al., 2013). With increasing dead wood diversity, sites can host more unique species assemblages including also specialists (Abrego and Salcedo, 2013; Nordén et al., 2013). Similar, although weaker trend occurred with *Micarea* lichens.

The species richness of decomposers or *Micarea* lichens was not affected by dead wood diversity or management intensity. Increased dead wood diversity should contribute to a higher amount of available resources and niches (Siitonen, 2001; Stokland et al., 2012), and its positive effect on species richness of wood-inhabiting fungi has been demonstrated in previous studies (e.g., Hottola et al., 2009; Penttilä et al., 2004; Similä et al., 2006). Also, the negative effects of management intensity have been widely reported (e.g., Arnstadt et al., 2016; Bader et al., 1995).

In studies where all dead wood diversity (including also different tree species) has been measured to reflect the stand continuity, and the species richness has been measured from all of the material contributing to the dead wood diversity, it is very logical that clear positive correlations occur between species richness and stand continuity (see for example Hottola et al., 2009; Penttilä et al., 2004; Similä et al., 2006). Thus, it is worth emphasizing that as we measured only the dead

wood diversity of pine, and recorded the fungal species richness only from the selected standing dead trees, such correlation might be more difficult to find. However, we argue that if such a correlation would be found it would truly reflect the species dependence on stand continuity, not just that more diverse substrate pool has more diverse species pool.

Species interactions might also play its part in the absence of a positive relationship between species richness and stand continuity. Heilmann-Clausen and Christensen (2005) found that the species richness of wood-inhabiting fungi on an individual tree was negatively affected by dead wood continuity (estimated as the proportion of strongly decayed logs). They suggested competitive exclusion to be one of the possible explanations: highly competitive specialists replace the early successional, non-specialist species in sites with high dead wood continuity. Thus, the species richness it not necessarily higher in the high continuity stands compared to stands with lower continuity, but can show no trends or even be lower.

In addition, the sites were located in or in the vicinity of conservation areas and thus, at least some natural forests were located in the proximity of sites. The variation in dead wood diversity and management intensity might not have been sufficient to reveal all existing trends. Moreover, management intensity of the sites was relatively low compared to the average managed forests in the area. In a study by Penttilä et al. (2004), dead wood diversity and management intensity induced a clear trend in polypore community composition when they compared communities in managed and old-growth forests. They recorded 400–500 stumps in managed stands, whereas the most managed site in this study included only 112 cut stumps per hectare.

The fact that stand continuity did not have a strong effect on decomposers and *Micarea* lichens gives indirect evidence that they are not dispersal limited at such fine spatial scales. In fact, it has been suggested that pine inhabiting fungi would be less affected by forest management than species specialized in e.g. spruce due to their better dispersal abilities (Stokland and Larsson, 2011). Stokland and Larsson (2011) hypothesized that this could be due to the different selection pressures

375 in pine forests that experience forest fires and have lower input rates of dead wood than spruce
376 forests. Thus, the sites may support viable metacommunities of these pine-inhabiting species if
377 landscape level continuity is high. However, on rare specialist species, dispersal limitations might
378 occur already at small spatial scales (Norros et al., 2012).
379
380 **4.2. Effects of microhabitat continuity**
381 *Micarea* species richness increased with time since tree death. Microhabitat continuity could be
382 more important for *Micarea* lichens than stand continuity due to their slow rates of growth and
383 establishment (Nordén et al., 2014; Stenroos et al., 2011). With increasing time since tree death
384 there is more time available for colonization (Johansson et al., 2007), and new suitable
385 microhabitats, such as decorticated wood appear (Renvall, 1995). The result also fits well with the
386 hypothesis of species time relationship (Rosenzweig, 1995), especially because competitive
387 exclusion has been suggested to be rare in lichens (Lawrey, 1991; Uliczka and Angelstam, 1999).
388 Species richness of decomposers was not affected by time since tree death. Previous studies
389 have demonstrated an increase in species richness of wood-inhabiting fungi from initial decay
390 stages to intermediate ones (Arnstadt et al., 2016; Renvall, 1995), and with time since tree death
391 (Heilmann-Clausen, 2001). This pattern could result from changes in the tree quality (e.g. bark
392 exfoliation (Renvall, 1995), and decreasing wood density in standing dead trees (Saint-Germain et
393 al., 2007)), and from the emergence of late successional species (Høiland and Bendiksen, 1997). In
394 the present study, the trunks with the longest time since their death probably included many kelo
395 trees, i.e. standing dead trees characterized by slow death that makes the trunk very resistant to
396 decay (Niemelä et al., 2002). Since kelos are utilized by a limited set of specialist species (Niemelä
397 et al., 2002; Stokland et al., 2012), species richness might not increase linearly with time.
398 Additionally, increasing competition with increasing habitat patch age might explain our result
399 (Nordén and Appelqvist, 2001).

Community composition of both decomposers and *Micarea* lichens was slightly dependent on time since tree death. Communities on recently died trunks probably share certain (pioneer) species that inhabit the freshly dead wood (Niemelä et al., 1995; Renvall, 1995). Later on, fungal succession takes place with proceeding decomposition (Rajala et al., 2012; Stokland et al., 2012) and thus, different species of wood-inhabiting fungi should occur at different times after the tree death (Niemelä et al., 1995; Heilmann-Clausen, 2001). Trends in the community composition could have been stronger if more trunks at the end of the decomposition range could have been included in the analyses. The trunks for which the year of death could not be determined due to the erosion of the outermost tree rings were likely the oldest but had to be excluded from our analyses.

Tree age at death did not affect either of the studied fungal groups. This indicates that it might be important only for few species if any. The opposite was hypothesized as, for example, the community composition of dead wood might be affected by the longevity of infection history during the tree lifespan (Heilmann-Clausen and Christensen, 2004). Similar to the tree age at death, trunk diameter did not affect the communities of wood-inhabiting fungi. Several studies focusing on downed dead wood have reported the opposite (e.g., Høiland and Bendiksen, 1997; Renvall, 1995). However, our results are in accordance with the results by Pouska et al. (2016a) that showed no effect of diameter on wood-inhabiting fungal communities on standing dead Norway spruces. They suggested that diameter interacts with several other, more important trunk characteristics (e.g. trunk temperature and moisture) than diameter *per se.*

Also canopy openness did not affect wood-inhabiting fungal communities. Sun exposure may affect community composition of wood-inhabiting fungi (Heilmann-Clausen, 2001), and lichens have been shown to respond positively to increasing canopy openness (Marmor et al., 2012; Uliczka and Angelstam, 1999). Our results could be explained by milder edge effect in natural forest edges (Ruete et al., 2016) that were characteristic for our study sites. Moreover, canopy

openness might be positively related to stand age, and thus light availability would not limit lichen communities in older stands (Bäcklund et al., 2016).

4.3. Conclusions

In the conservation areas of central Finland, wood-inhabiting fungal diversity was not significantly affected by local forest continuity. The results indicate that on a stand scale, other environmental filters and stochastic processes underlie the patterns of wood-inhabiting fungal diversity on standing dead pines. Although some species would depend on the continuous supply of dead wood and old trees, they seem not to be limited by dispersal, and can find these suitable habitats within the surrounding landscapes, underlining the importance of landscape level continuity.

The results demonstrated the importance of old, standing dead trees for species-rich communities of *Micarea* lichens. Conservation strategies concerning these species should aim to increase the local number of old trees that die and decay naturally. To achieve this, approaches of retention forestry should be applied in managed forests (Gustafsson et al., 2012; Lindenmayer et al., 2012). However, increasing the number of veteran trees in forest landscapes requires extending the time-frames of strategies that are currently applied in forest management (Lindenmayer et al., 2014).

The explicit relationship between local continuity and rare species remained unsolved. These species might be more sensitive to local continuity than common species when taking into consideration e.g. their highly specialized habitat use (Nordén et al., 2013). Therefore, rare and red-listed species should be at the center of future research on local continuity to be able to guide the required conservation actions, and to maintain these species also locally.

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APPENDIX A. Supplementary tables (Table A.1–A.3).

APPENDIX B. Responses of individual species

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